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Modeling the distribution of Norway rats (*Rattus norvegicus*) on offshore islands in the Falkland Islands

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Abstract

Non-native rats (*Rattus spp.*) threaten native island species worldwide. Efforts to eradicate them from islands have increased in frequency and become more ambitious in recent years. However, the long-term success of some eradication efforts has been compromised by the ability of rats, particularly Norway rats (*Rattus norvegicus*) which are good swimmers, to recolonize islands following eradications. In the Falkland Islands, an archipelago in the South Atlantic Ocean, the distance of 250 m between islands (once suggested as the minimum separation distance for an effective barrier to recolonization) has shown to be insufficient. Norway rats are present on about half of the 503 islands in the Falklands. Bird diversity is lower on islands with rats and two vulnerable passerine species, *Troglodytes cobbi* (the only endemic Falkland Islands passerine) and *Cinclodes antarcticus*, have greatly reduced abundances and/or are absent on islands with rats. We used logistic regression models to investigate the potential factors that may determine the presence of Norway rats on 158 islands in the Falkland Islands. Our models included island area, distance to the nearest rat-infested island, island location, and the history of island use by humans as driving variables. Models best supported by data included only distance to the nearest potential source of rats and island area, but the relative magnitude of the effect of distance and area on the presence of rats varied depending on whether islands were in the eastern or western sector of the archipelago. The human use of an island was not a significant parameter in any models. A very large fraction (72%) of islands within 500 m of the nearest potential rat source had rats, but 97% of islands farther than 1,000 m away from potential rat sources were free of rats.

Keywords

Invasive species; eradication; *Rattus norvegicus*; metapopulation

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Introduction

Introduced species can have detrimental consequences for native island communities (Wiles et al. 2003, Kurle et al. 2008) and rats are among the most problematic species introduced to islands (Hilton and Cuthbert 2010). Three species of rats (*Rattus norvegicus*, *R. rattus*, and *R. exulans*) live as commensals of humans. As a result of human-aided dispersal (Blackburn et al. 2004), these rodents are found on a very large fraction of the world's islands (King 1985) where they often have negative consequences for native species (Atkinson 1985). Rats can cause population declines and even the extinction of many species of island birds, amphibians, and reptiles (Towns et al. 2006, Cree et al. 1985). Eradicating rats from islands can lead to the recovery of native species and many of the ecological processes that they mediate. For example, between 12 and 22 years after rats were removed from several islands in New Zealand, population densities of seabirds recovered and their increase was accompanied by gains in soil nitrogen content (Jones 2010). Rats disperse to islands with human assistance, but they can also move among islands by themselves (Russell et al. 2010, Russell and Clout 2004). Norway rats (*R. norvegicus*) are particularly good swimmers and can reinvade eradicated islands (Russell et al. 2008). To eradicate rats successfully and permanently, it is necessary to understand the factors that determine their capacity to colonize islands (Fewster et al. 2011).

Norway rats (*Rattus norvegicus*) were introduced to the Falkland Islands (or "Falklands") in the 18th century (Poncet et al. 2011). They are present on the two largest islands, East and West Falkland, and about 235 of 503 smaller offshore islands that comprise the archipelago (Falkland Islands Government 2013). The Falkland Islands are situated in the southwest South Atlantic Ocean between latitudes of 51°S and 53°S and 57°30'W and 61°30'W. They occupy 12,173 km^2 of land and in 2012 had a human population of 2,932 inhabitants (Falkland Islands Government 2012). In addition to the introduction of Norway rats (henceforth referred to as "rats"), the Falklands have undergone significant ecological changes since the 18th century. These ecological changes include overgrazing with concomitant vegetation changes (McAdam 1980), increased fire frequency (Armstrong 1994, Woods and Woods 2006), climate change (Bokhorst et al. 2007), and declines in the abundance of marine mammals and seabirds throughout the archipelago (Palomares et al. 2006, Strange 1992). The pattern of human movement and activity on the islands has also varied since the arrival of sealers and whalers in the early 18th century and the establishment of the first permanent settlements in the 1760s (Strange 1992). Many, if not all, of these factors have likely influenced the distribution of rats.

The presence of rats in the Falkland Islands is associated with a significant reduction in the diversity and abundance of passerine birds (Hall et al. 2002, Tabak et al. 2014). Two species of passerines are particularly sensitive to rats. Cobb's wren (*Troglodytes cobbi,* Fig. 1), the only endemic land bird species of the Falklands, is absent from islands in

Figure 1. Two bird species of conservation concern in the Falkland Islands. Cobb's wren (**A**) and Tussacbird (**B**) are both highly vulnerable to the presence of rats. Protecting these species from local extinction requires effective management in the Falkland Islands, including the eradication of Norway rats.

which rats are present. Cobb's wren is considered a vulnerable species by the International Union for the Conservation of Nature (IUCN 2012). Tussacbird (*Cinclodes antarcticus,* Fig. 1) is found very rarely on islands with rats and, when they are present, their abundance is much lower than that observed on islands free of rats (Tabak et al. 2014). This species is only found in the Falkland Islands and on rat-free islands of the southern tip of South America (Strange 1992, Pina and Cifuentes 2004). Protection of these two species requires the maintenance of rat free islands in the Falkland Islands. Rat eradications appear to benefit the diversity of native passerine birds in the Falklands (Tabak et al. 2014a), but eradication efforts are hampered by the ability of rats to swim between islands.

Brown (2001) suggested that if an island in the Falkland Islands was at least 250 m (later revised to 350 m) from the nearest rat-infested island, it was likely to be safe to eradicate rats from this island because rats would not reinvade by swimming. These threshold distances were derived from physiological experiments on the maximum swimming distance of rats at different temperatures. Sea surface water temperature in the Falklands ranges from 5 to 8 °C (Waluda et al. 1999; Agnew et al. 2000). The length of time that Norway rats can survive in water decreases with temperature. At 9 °C, this time is about 9 ± 1 min (Le Blanc 1958). The maximum speed Norway rats have been recorded swimming in the laboratory is 1.4 km/h (Dagg and Windsor 1972). Therefore, assuming that Norway rats can survive in Falkland Islands seawater for ten minutes and that they swim their maximum speed this entire time, their estimated maximum swim distance is 233 m. The estimates of 250 to 350 m were conservative based on laboratory studies.

Since 2001, 66 islands in the Falklands have been successfully treated for rat eradication. However, rats have reinvaded 10 of the islands from which they were eradicated (Falkland Islands Government 2013; Fig. 2), suggesting that this threshold distance for preventing reinvasions is too low. Tabak et al. (2014b) used population genetic

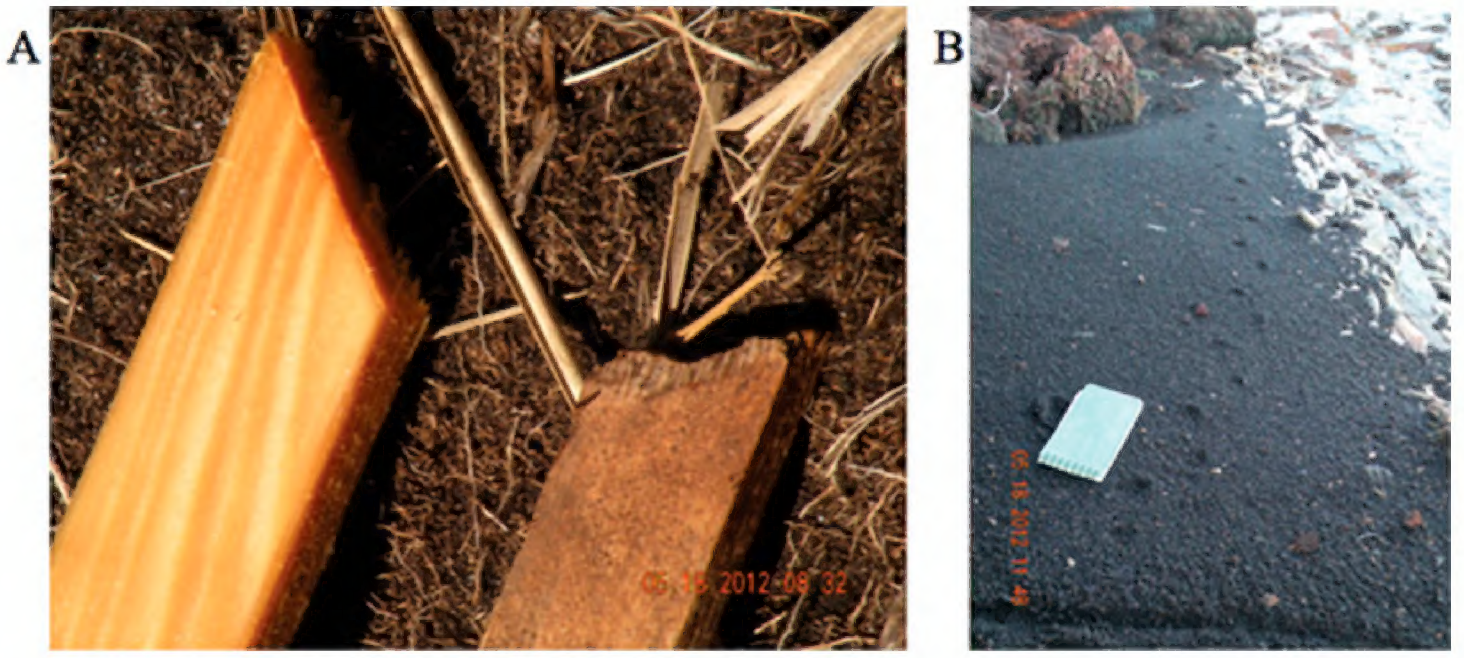

Figure 2. Evidence for rat reinvasion following eradication. Gnawed chewsticks (**A**, right) and rat tracks (**B**) indicate that an island has been reinvaded by rats. Chewsticks are wood pieces soaked in edible oil. They are useful and cost-effective tools used to determine if an eradication attempt was effective at removing rats and to determine if rats have returned to an island after a successful eradication.

analyses to estimate how far rats tend to move between islands in the Falkland Islands. They found evidence of significant migration, and hence presumably rats swimming, distances of up to 830 m. They suggested that 830–1,000 m was a conservative distance for safe and effective eradication. Our study complements the work of Tabak et al. (2014b) by our use of occupancy modeling based on the distribution of rats and the distance to the nearest rat source to estimate the maximum swimming distance of rats between islands.

Here we examined the relationship between the presence of Norway rats and island characteristics in the Falkland Islands. To guide our analyses, we conceived of rats in the Falklands as a metapopulation in which island sub-populations are linked by dispersal, and in which the presence of rats is determined by the balance between colonization and extinction among islands (Fronhoffer et al. 2012). Following this classical view of metapopulations (Levins 1969, 1970), we hypothesized that the presence of rats would decrease with distance from the nearest island with rats, the island presumably functioning as a reservoir and source of rats (for the purposes of this manuscript, we use "source" to describe any island on which rats are present). We also hypothesized that rats would be found more often on larger than on smaller islands (Hanski et al. 1996). Larger islands are more likely to be visited by humans, represent a larger colonization target, and presumably maintain larger rat populations that are less likely to become locally extinct than smaller islands (Russell and Clout 2004). In addition to these two major variables, we examined the potential roles of geographic location and human presence on the prevalence of rats on islands, as humans tend to carry rats when they travel to islands (Atkinson 1985).

Methods

Our analysis included 158 islands, 56 of which had rats and 102 of which had no evidence of rats (Fig. 3). None of the islands in this analysis had been the subject of eradication programs. Islands ranged in size from 0.3 ha to 5,585 ha. Data for rat status (presence or absence) on each island, island surface area, and the geographic location of each island (east or west sector of the archipelago) were obtained from the Falkland Islands Biodiversity Database (Falkland Islands Government 2013). Surveyors walked at least 1 km along the coast and assessed the presence of rats based on fresh sign (i.e., droppings, tracks, sightings of live animals, and rats caught in traps). It is possible that rats were present on some islands, but not detected in surveys (Mackenzie et al. 2002). Therefore, we estimated the detection probability of rats by conducting 5 repeated surveys on each of 10 randomly selected islands in the Falkland Islands from 30 March–27 April 2013.

Data for human activity on each island were obtained from the Falkland Islands Biodiversity Database (Falkland Islands Government 2013). Human use is defined as the use (both historical and contemporary) of an island by humans for activities involving temporary or permanent occupation of the island and landing of livestock, building materials, and other goods. Most of these activities in the Falkland Islands are traditionally associated with grazing of livestock. We ranked the intensity of human use into 5 categories according to the type of occupation or use: 0 (island has never had grazing nor structures and there has never been temporary nor permanent human occupation or use); 1 (island has been grazed but no structures have been built and the island has no history of temporary nor permanent occupation by humans); 2 (island has been grazed and minor structures [i.e., fences or corrals but not woolsheds, huts, or houses] have been built and there has never been temporary nor permanent human occupation); 3 (island has been grazed, minor structures and major structures [i.e., woolsheds, huts, or houses] have been built, and the island has been occupied temporarily but never year round); and 4 (island has been grazed, minor and major structures have been built, and the island has been occupied year round).

To determine if island location had an effect on the probability of rat occupancy, we allocated islands to one of two geographical sectors: western or eastern. We separated the islands into sectors by measuring the straight-line distance between each island (*i*) and East Falkland (*e*) and West Falkland (*w*) using maps published by the Directorate of Overseas Surveys (1961) with a resolution of 1:50,000. If the distance from island *i* to East Falkland (D_{ie}) was less than the distance to West Falkland (D_{iw}), we assigned this island to the eastern sector. If $D_{iw} < D_{ie}$, we assigned island *i* to the western sector. For each island, we identified the nearest rat source (or potential source) by measuring the straight-line distance from each island (*i*) to the nearest rat-infested island (*j*) and the second-nearest rat infested island (*k*) using maps published by the Directorate of Overseas Surveys (1961) with a resolution of 1:50,000.

To identify the most important variables that predict rat distribution in the Falkland Islands, we constructed a collection of nested generalized linear models (GLMs) using

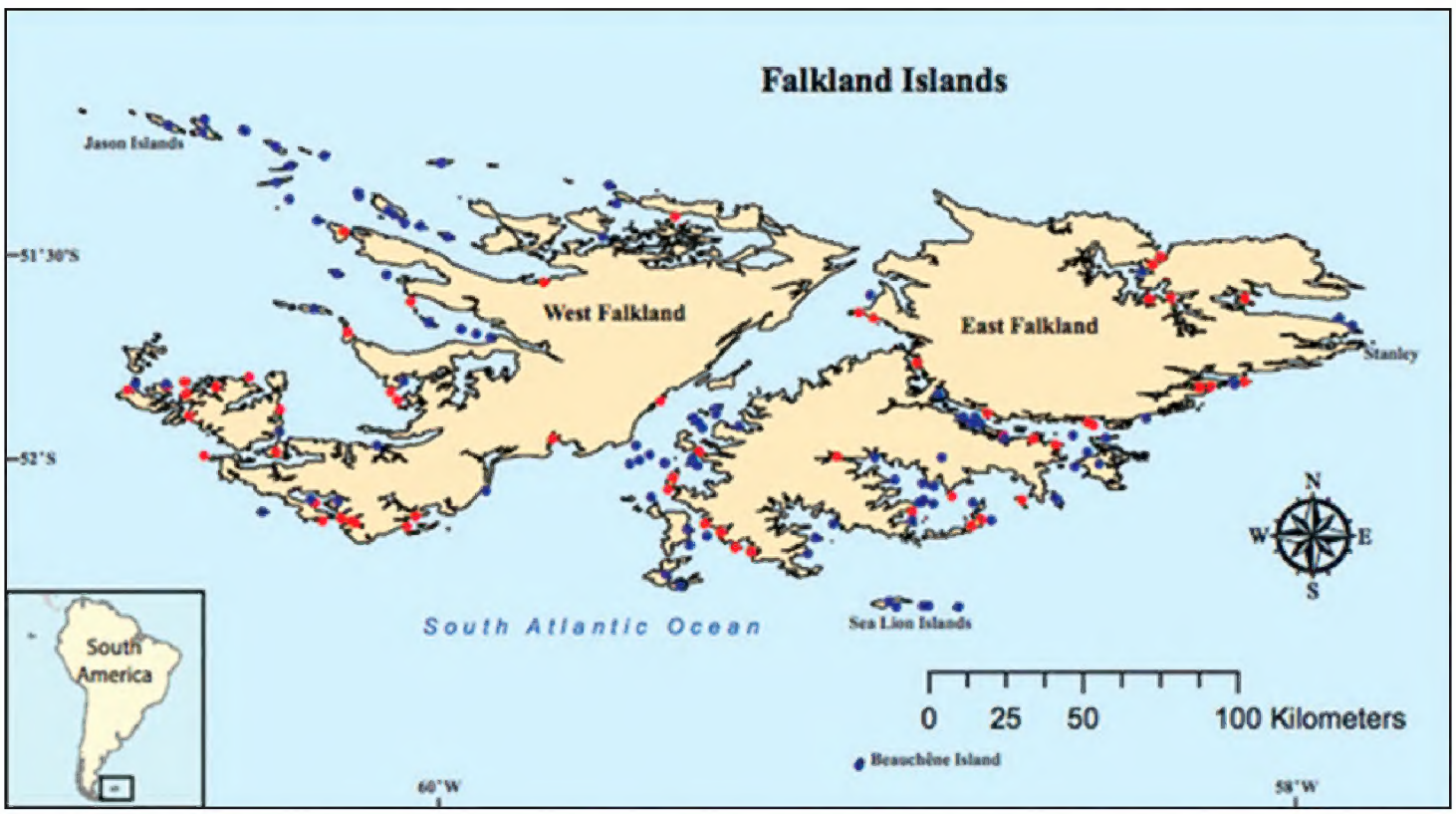

Figure 3. Distribution map of Norway rats in the Falkland Islands. Islands with rats (red points) appear in clusters. We hypothesize that rats are able to move between islands that are geographically close. Islands without rats (blue points) are typically farther from the mainland (East and West Falkland). Islands were assigned to geographic sectors based on their location: islands closer to West Falkland are in the western sector, while islands closer to East Falkland are in the eastern sector.

rat presence or absence as response variables. The full and most complex model included as independent variables the following four factors: $\log_2$-transformed distance to the nearest rat-infested island (*Log_2Dist*), $\log_{10}$-transformed island area (*$Log_{10}A$*), human use (*HumUse*), and geographic sector (eastern or western; *West*). Because island area ranged from 1 to over 5,000 ha, we log-transformed data using base 10. This transformation allowed us also to compare graphically with data on other islands and in other publications ($\log_{10}$ is traditionally used in island biogeography studies; MacArthur and Wilson 1967; Morley and Winder 2013). We used a base 2 logarithmic transformation for distances as it allowed easier visualization of the shorter distances that we wanted to emphasize for comparison with the estimated maximal distance that rats were supposed to swim (i.e., less than 500 m). The full model also included all possible pairwise interactions between these predictor variables. We compared these models using AIC_C scores and chose the model with the lowest score as the model best supported by data. For each of the models we fitted in the analyses, we estimated Nagelkerke's pseudo-R^2 (N-R^2) as a qualitative measure of goodness of fit (Nagelkerke 1991). For each of these models we also tested for overdispersion ($d > 1$; Moore 1986). When multiple models had similar levels of support ($\Delta AIC_C < 2$) we calculated predicted values associated with each of the alternative models (Anderson 2008). Because we favor parsimony in our models, if the differences between predicted values were very small and models had similar levels of support ($\Delta AIC_C < 2$) we chose the simpler of models (i.e., the model with fewer variables; Burnham and Anderson 2002). Our models do not consider the potential role of shipwrecks in dispersing

rats because data on the history of shipwrecks are not available for each island. However, 13 of the 158 islands analyzed are known to have shipwrecks off their shore (Southby-Tailyour 1985). Of these, only 3 islands are rat infested.

Results

We found that rats were present on 5 of the 10 islands that were surveyed repeatedly. On islands where rats or their sign were found to be present, rats (or their sign) were detected in each of the 5 repeated surveys. They were not found in any repeated surveys of islands determined to be rat-free. Therefore, the detection probability of rats in the Falkland Islands can be assumed to be close to 100%.

The model best supported by the data included an effect of distance to the nearest rat-infested island, island area, and geographical sector (Table 1). The probability of rat occupancy decreased with distance to the nearest rat source, increased with island area, and was higher in the western sector. The overdispersion parameter was not significant for this model ($p = 0.95$). None of the models that were best supported by the data included human use ($\Delta AIC_C > 2$). Since there was a significant effect of the geographical sector in the model, we separated the islands into two sectors (eastern and western sectors) and ran the models separately for each of them. When we analyzed the data separately for each geographical sector, in all of the best-supported models, rat occupancy decreased with distance to the nearest rat-infested island (Tables 2 and 3). In the western sector, two models had substantial support ($\Delta AIC_C < 2$, Table 2). These models both included distance to the nearest rat source and island area as effects, but one included an interaction between these variables, while the other did not. We calculated the difference between the predicted values associated with these models. Because the mean difference in the values predicted by the two alternative models was very small (0.0022 ± 0.083 (SD)), we chose the simpler of the two models. This model included an effect of the log of island area as well as the log of the distance to the nearest rat source, but no interaction term (Fig. 4). In contrast, for islands in the eastern sector, three models were well supported by the data ($\Delta AIC_C < 1$, Table 3). We calculated the differences associated with the predicted values for each pair of models. The average difference between the predictions of pairs of models was very low ($1.73 \times 10^{-9} \pm 1.35 \times 10^{-11}$ (SD)). We concluded that the models were not biologically different and chose the simplest of the three models. The only parameter in the model selected for islands in the eastern sector was the log of distance to the nearest rat-infested island (Fig. 4).

In the western sector, the odds of rat presence increased by a factor of about 8.9 for each 10-fold increase in island area. In the eastern sector, the best model did not include an effect of island area. The effect of swim distance differed between eastern and western sectors. In the east, for every doubling of the distance to the nearest rat-infested island the odds of rat presence decreased by a factor of 0.36, whereas in the west, doubling the distance to the nearest rat source decreased the odds of rat occupancy by a factor of 0.09.

Table 1. Models predicting the Probability of rat presence (π).

Model	AIC_C	ΔAIC_C	$N\text{-}R^2$
logit (π) = 12.67 - 1.42**Log*$_2$*Dist* + 0.80**West* + 0.54* *Log*$_{10}$*A* - 0.34*(*Log*$_2$*Dist* - 10.25)X(*Log*$_{10}$*A* - 1.29)	118.78	0	0.62
logit (π) = 11.55 - 1.36* *Log*$_2$*Dist* + 0.78West* + 0.83* *Log*$_{10}$*A***	**119.48**	**0.7**	**0.61**
logit (π) = 12.26 - 1.42* *Log*$_2$*Dist* + 0.60**West* + 0.84* *Log*$_{10}$*A* - 0.24*(*LogDist* - 10.25)X*West*	120.42	1.64	0.61
logit (π) = 11.53 - 1.36* *Log*$_2$*Dist* + 0.79**West* + 0.82* *Log*$_{10}$*A* + 0.02**HumUse*	121.61	2.83	0.61
logit (π) = 11.90 - 1.41* *Log*$_2$*Dist* + 0.84**West* + 0.92* *Log*$_{10}$*A* - 0.38*(*Log*$_{10}$*A* - 1.29)X*West*	123.34	4.56	0.62

Probability of rat presence (π) was best predicted by the logarithm of distance to the nearest rat-infested island (*Log*$_2$*Dist*), the nearest large landmass (East or West Falkland; *West*), and the logarithm of island area (*Log*$_{10}$*A*).

Table 2. Models predicting the Probability of rat presence (π) for the west half of the archipelago.

Model	AIC_C	ΔAIC_C	$N\text{-}R^2$
logit (π) = 27.49 - 2.91* *Log*$_2$*Dist* + 1.75* *Log*$_{10}$*A* - 0.92*(*Log*$_2$*Dist* - 1.45)X(*Log*$_{10}$*A* - 10.75)	32.84	0	0.84
logit (π) = 20.66 - 2.36* *Log*$_2$*Dist* + 2.19* *Log*$_{10}$*A*	**33.91**	**1.07**	**0.82**
logit (π) = 14.19 - 1.45* *Log*$_2$*Dist*	46.05	13.21	0.69
logit (π) = -0.34 - 0.02* *Log*$_{10}$*A*	93.49	60.65	0.0003

For the west half of the archipelago, the probability of rat occupancy decreased with the distance to the nearest rat-infested island (*Log*$_2$*Dist*) and increased with the logarithm of island area (*Log*$_{10}$*A*).

Table 3. Models predicting the Probability of rat presence (π) for the east half of the archipelago.

Model	AIC_C	ΔAIC_C	$N\text{-}R^2$
logit (π) = 8.72 - 1.02* *Log*$_2$*Dist*	**82.93**	**0**	**0.44**
logit (π) = 8.72 - 1.07* *Log*$_2$*Dist* + 0.42* *Log*$_{10}$*A*	83.34	0.41	0.46
logit (π) = 10.11 - 1.18* *Log*$_2$*Dist* + 0.12* *Log*$_{10}$*A* - 0.36*(*Log*$_2$*Dist* - 9.89)X(*Log*$_{10}$*A* - 1.78)	83.76	0.83	0.48
logit (π) = -0.71 + 0.021* *Log*$_{10}$*A*	117.27	34.34	0.0001

In the east half of the archipelago, the probability of rat occupancy decreased with distance to the nearest rat-infested island (*Log*$_2$*Dist*). There was also substantial support for the model that predicted occupancy would increase with the logarithm of island area (*Log*$_{10}$*A*), however we chose the simpler of the two models.

Discussion

Our results indicate that the incidence of rats decreased with distance to the nearest rat-infested island. Also, for islands in the western sector of the archipelago, we found that the probability of rat occupancy increased with island area. In the eastern sector, we did not find a significant effect of island area on rat presence. Human activity did not appear to be a significant variable in the models, suggesting that it is not as important in determining the distribution of rats as distance from sources and island area. Here we consider the possible processes that might have produced these patterns. Specifically, we explore whether the observed patterns might be shaped by the balance between colonization and extinction as the classical metapopulation model suggests (Hanski et al. 1995), and argue that rats in the Falkland Islands satisfy some of the assumptions

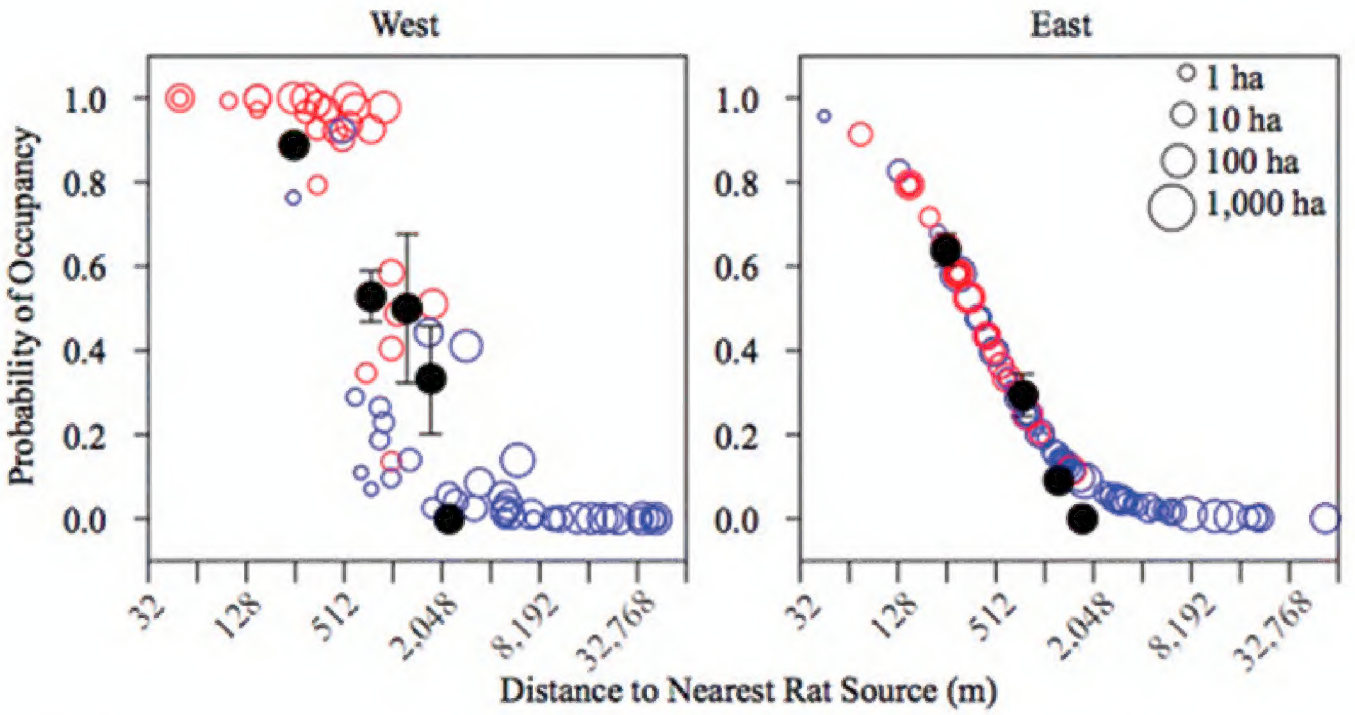

Figure 4. Models for rat distribution included distance to the nearest rat source and island size. This figure presents the fraction of islands of a given size (bubble size is proportional to island size) predicted to have rats by our models as a function of distance to the nearest rat source. Colors of dots represent islands with (red) or without rats (blue). In both the west and east of the Falkland archipelago, the probability of rat presence on an island decreased with distance to the nearest rat-infested island. There was a higher probability of rat presence in the western sector than in the eastern sector and in the west rats were more likely to be found on larger than on smaller islands. In the east, there was no significant effect of island area on rat occupancy. Black dots (± SE) represent the fraction of islands with rats binned in groups of 500 m of swim distance.

of this model. To illustrate, we present preliminary evidence that rats migrate between islands in the Falklands, and that rat populations can go extinct. Then, we consider the implications of our data and models to management of rats in the Falklands.

Interpreting models

The models that we used to analyze the factors that determine the presence of rats in the Falkland Islands are descriptive. They document patterns, but by themselves, they do not reveal the processes that create them (Clinchy et al. 2002). Similar models are widely used in the study of metapopulations and can be used to estimate a variety of parameters, including extinction and colonization rates, from a snapshot of presence/absence data (Driscoll 2007). Our data do not satisfy many of the assumptions needed to make these estimates. First, presence or absence of rats was assessed not as a snapshot, but over a period of several years (Falkland Islands Government 2013). Second, we only have data for a subset of islands and hence have to rely on distance to the nearest rat-infested island rather than on the distances to all possible island sources of rats for a focal island. Nevertheless, our data and results are consistent with the idea that rats in the Falklands represent a metapopulation.

As predicted by all classical metapopulation models (Hanski 2004), the occurrence of rats decreased with distance to potential rat sources. This result together with anecdotal observations suggests that rat subpopulations are linked by dispersal, but that exchanges of rats are more likely between adjacent rather than distant islands. Field observations support the conjecture that rats can move between subpopulations. For example, rats were successfully eradicated from Rookery Island in 2002 (and confirmed absent three years later using chew sticks), but eight years later we visited the island and found abundant fresh rat sign (Fig. 2). The most likely source of rats is Rat Island, 500 m away. Similar reinvasions have now been recorded on 8 islands between 2 and 6 years following successful eradication, over distances of up to 500 m (Falkland Islands Government 2012). It is more difficult to show that rat sub-populations go extinct, but 7 islands on which rats are currently known to be absent seemingly exhibit the legacy of being occupied by rats, with the absence of *T. cobbi* and low densities or absences of *C. antarcticus*, conditions which are otherwise only found on islands with rats present or shortly following rat eradication (Tabak et al. 2014a). It is possible that these islands had rats recently but that their local populations became extinct.

Although rats likely colonize islands and go locally extinct on islands, we doubt that the patterns of rat distribution revealed by our dataset are solely the steady state outcome of colonization and extinction. It is likely that these processes continue to occur, but it is also likely that the patterns that we have documented are the result of the interplay of environmental factors, both contemporary and historical. Nevertheless, human activity was not a significant variable in the models, suggesting that it is less important than distance to sources and island area. Russell and Clout (2004) also reported no correlation between an anthropogenic variable and Norway rat distribution in New Zealand. It appears that swimming is the most important mechanism by which rats move between islands in the Falklands.

How far can rats swim among islands?

The swimming abilities of rats are poorly understood but remarkably important, because they determine whether and when rats will reinvade islands that have been eradicated (Russell et al. 2010). The prevalence of rats decreased with distance from potential sources (Fig. 4), and very few islands further than 1 km away from a potential source of rats appeared to have been invaded. However, about 72% of the 54 islands within 500 m from the nearest source had rats, about 40% of 34 islands between 500 and 1,000 m away had rats on them, and of the 69 islands farther than 1,000 m from the nearest source, only two had rat populations (Table 4). Rats are also known to have swum at least 500 m to reinvade an island successfully cleared of rats (Falkland Islands Government 2013). This suggests that although there are limitations to how far rats can move among islands, these animals can swim relatively long distances, and consid-

Table 4. Proportion of islands occupied by rats at different distances from the nearest source.

Distance between islands (m)	Percent of islands occupied rats (%)
< 500	72
500–1,000	40
≥ 1,000	3

The probability of rat occupancy decreased with distance to the nearest rat source. Beyond 1,000 m, there was a low probability of rat occupancy.

erably farther that the 250 m initially suggested as a possible safe separation distance for eradication in the Falkland Islands (Brown 2001).

These results are surprising as the swimming endurance of rats decreases with water temperature and sea-surface temperatures in the Falkland Islands are cold (ranging from 2 °C in winter to 10° C in summer; Otley et al. 2008). At those temperatures, rats in the laboratory can only swim for less than 10 minutes (reviewed by Russell et al. 2008). Assuming a maximal speed of ≈ 25 m/min (Møller 1983), rats could potentially swim only between islands that are less than 250 m apart. Our data suggest that either Falklands rats are both hardier and better swimmers than laboratory rats or Falklands rats are frequently carried distances much larger than laboratory rats by oceanic currents. Rats in the Falklands appear capable of swimming relatively frequently (at least in ecological time) between islands separated by 500 m. Consequently, they might be able to swim even longer distances on occasion. Although the probability of a rat surviving a long distance swim and establishing a viable breeding population may be extremely low, the cumulative probability will increase over time. Factors that precipitate dispersal are unknown in the Falklands. One possible explanation is that rats swim to islands where whale strandings have recently occurred. These events provide an abundance of food for rats and occur with regular frequency in the Falklands (Otley 2012). Hypothetically, rats could smell these whale strandings from nearby islands and swim to this food source (Harper 2005). Another possible explanation is that large storms might facilitate rat dispersal (Losos et al. 1993).

Implications for management

Norway rats have reinvaded islands following eradications in the Falklands and in other archipelagoes. For example, three species of rats were eradicated from Perl Island, New Zealand in 2005 and Norway rats re-established a population across the island by 2007 (Russell et al. 2010). A relatively large proportion (29%) of islands from which Norway rats have been eradicated in New Zealand have been reinvaded (Clout and Russell 2006, Russell et al. 2008). Cost effective rat management strategies must account for the possibility that rats will reinvade after eradications, and must attempt to minimize this possibility. Although we cannot estimate with precision the rates of

rat colonization and dispersal among islands, nor the effect that distance and island area have on these, our data and results can still inform active rat eradication efforts in the Falklands.

Our models suggest that islands farther than 1,000 meters from the nearest rat-infested islands have a low probability (less than 0.05) of having rats, and hence of having been invaded. Indeed, of the 69 islands that are farther than 1,000 m from the nearest rat source in our dataset, only 2 have rat populations. We think that 1 km away from the nearest rat source is a reasonable threshold for eradication. This threshold does not guarantee that these islands will remain rat-free in perpetuity, but it represents a reasonable threshold that ensures a low probability of reinvasion after eradication (Russell et al. 2008).

Our data confirm the ability of rats to disperse among islands that are close to each other. If two or more islands are sufficiently close to each other as to have a high probability of reciprocal re-invasion, from a management perspective, these islands form a single "eradication unit," requiring simultaneous baiting (Robertson and Gemmel 2004). Eradication units can be informed by genetic profiling of different island populations (Abdelkrim et al. 2005). In a genetic profile of Falkland Islands rats, Tabak et al. (2014b) found that rats are capable of swimming distances of at least 830 m. We find the congruence between our current estimate of 1,000 m and the previous estimate of 830 m evidence of the robustness of these estimates. We argue that a threshold distance of 830–1,000 m is safe for eradication with a low probability that rats will recolonize. However, we recommend that prior to eradication attempts, rats on candidate islands and nearby rat-infested islands are sampled for genetic analyses to ensure that migration does not occur from rat sources to the candidate island.

Conclusion

Eradication of invasive rats can be an effective conservation tool, but the propensity of rats to return to islands following eradication can hamper the effectiveness of this strategy. We found, by modeling the distribution of Norway rats in the Falkland Islands, that rats are capable of moving, presumably by swimming, between islands. When we compared our estimate with the literature, we conclude that rats are unlikely to move distances of greater than 830-1,000 m between islands in the Falklands. We suggest the use of this distance for future eradication plans.

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